Non-geographic variation in *Aethomys chrysophilus* (De Winton, 1897) and *A. namaquensis* (A. Smith, 1834) (Rodentia: Muridae) from southern Africa

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Prior to a systematic revision of African rock rats (genus *Aethomys* Thomas) in southern Africa, the nature and extent of non-geographic variation due to sex and age in two samples each of *A. chrysophilus* (De Winton, 1897) and *A. namaquensis* (A. Smith, 1834) were examined using both univariate and multivariate statistical procedures. Results of Model I two-way analysis of variance, % sum of squares and a series of multivariate procedures were congruent and showed a lack of sexual dimorphism in all samples examined, but marked variation between seven age categories based on the degree of tooth wear on the maxillary tooth row. When univariate and multivariate results were considered together, pooling of sexes as well as individuals of tooth-wear classes IV, V and VI for subsequent recording and analysis was justified. Very few tooth-wear class VII individuals were available and their exclusion was largely arbitrary. Few measurements showed sex-age interaction. The largest per cent contribution to the total variance was due to *error*. In general, variance partitioning indicated that if comparisons are to be made, caution needs to be exercised on the type of characters, number of factor levels and methodology used.

Voor 'n sistematiese hersiening van Afrika-kliprotte in Suider-Afrika (genus *Aethomys* Thomas) onderneem is, is die aard en omvang van nie-geografiese variasie toeskryfbaar aan geslag en ouderdom by twee monsters elk van *A. chrysophilus* (De Winton, 1897) en *A. namaquensis* (A. Smith, 1834) deur middel van beide eenveranderlike en meerveranderlike statistiese prosedures ondersoek. Resultate van Model I variansie-analise, % som van kwadrate en 'n reeks meerveranderlike prosedures het ooreengestem, en het die gebrek aan geslagsdimorfisme by al die monsters wat ondersoek is uitgewys, asook dat beide grootte- en vormvariasie tussen sewe ouderdomskategorieë voorkom wat op tandslytasie van die maksilêre tandry gegrond is. By die vertolking van beide eenveranderlike en meerveranderlike resultate in 'n breër konteks, was die samevoeging van geslagte sowel as individue van ouderdomsklasse IV, V en VI vir daaropvolgende optekening en analises geregverdig. Baie min individue van ouderdomsklas VII was beskikbaar en hul uitsluiting was arbitrêr. Min karakters het geslag-ouderdom interaksie getoon. Die hoogste persentasie bydrae tot die totale variansie was aan *fout* toe te skryf. Oor die algemeen het variansieverdeling getoon dat indien geldige vergelykings getref wil word, die tipe karakters, aantal faktore en metodologie wat toegepas word, omsigtig benader moet word.

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As part of a systematic revision of African rock rats of the genus *Aethomys* Thomas, the present study examines non-geographic variation in two species, *A. chrysophilus* (De Winton, 1897) (*sensu lato*, see below) and *A. namaquensis* (A. Smith, 1834), from four localities in southern Africa. The assessment of non-geographic variation is of particular importance in morphometric studies of geographic variation, and in the morphometric delineation of taxa (Thorpe 1976; Van der Straeten & Dieterlen 1992). Decisions regarding the components of variation to consider for statistical evaluation are of fundamental importance (Straney 1978). While some authors (e.g. Leamy & Bader 1968; Mayr 1969) consider non-geographic variation to be composed of genetic and non-genetic components, most workers view it as a function of differences in, for example, sex, age, season, cohort, and individuals within populations (Thorpe 1976; Straney 1978; Leamy 1983; Webster & Jones 1985; Dippenaar & Rautenbach 1986; Van der Straeten & Dieterlen 1992).

Non-geographic variation has, in the past, been assessed by a variety of univariate statistics and procedures such as the coefficient of variation (Genoways & Jones 1972), multiple *t*-tests (Straney 1978) and two-way analysis of variance (Robbins 1973), but their application has been criticized (Straney 1978; Leamy 1983). Two novel methods that rely either on the partitioning of variance components (Straney 1978) or the per cent contribution of the sum of squares (% *SSQ*) of each source of variation to the total *SSQ* (Leamy 1983), have been proposed more recently. The former method is computationally involved, but yields results that are generally comparable to the latter, which can be computed directly from a conventional two-way ANOVA table. Willig, Owen & Colbert (1986) expressed reservations about the univariate approach, arguing that significance tests for equality of means for each variable independently present the dilemma of having to consider the number of characters that must exhibit significance before overall significance is declared. They recommend the use of multivariate analysis of variance for evaluating overall group differences since it utilizes rather than ignores correlations among variables.

Some workers have attempted to adjust for sexually dimorphic and age-influenced characters (e.g. Cheverud

1982) by regression analyses of transformed characters (Thorpe 1976; Reist 1985) or by principal component analysis (Leamy & Thorpe 1984; Somers 1986). Such adjustments, however, require adequate samples from throughout the study area (Thorpe 1976; Dippenaar & Rautenbach 1986), a requirement hardly ever met by small mammal data sets. As an alternative to the sampling problem, other workers have attempted to pool geographic samples, but this is a dubious practice (Dippenaar & Rautenbach 1986).

This study evaluates non-geographic variation at the level of sexual dimorphism and age variation using the *SSQ* approach (and for comparison Model I two-way analysis of variance) and a series of multivariate procedures, with the objective of establishing criteria for the selection of specimens to consider for measurement recording and analysis in subsequent studies.

Material and Methods

The present study is based on samples of *A. namaquensis* from Boekenhoutkloof, Transvaal (25°31'S, 28°30'E; 25 males, 23 females), and Farm Narap, 28 km SSE of Springbok, Cape Province (29°53'S, 17°45'E; 15 males, 17 females), and *A. chrysophilus* from Farm Al-te-ver, 1 km SSE of Maasstroom, Transvaal (22°46'S, 28°28'E; 9 males, 13 females), and Olifantspoort Farm 328, 19,2 km S of Rustenburg, Transvaal (25°46'S, 27°16'E; 13 males, 8 females), South Africa. Specimens examined are listed in Appendix 1. The homogeneity of the samples of *A. chrysophilus (sensu lato)*, which is apparently composed of two sibling species (Gordon & Rautenbach 1980; Gordon & Watson 1986; Visser & Robinson 1986; 1987; Breed, Cox, Leigh & Hawkins 1988), was confirmed by preliminary analyses of cytogenetically known specimens.

Examination of the maxillary tooth-row, with reference to Verheyen & Bracke (1966), Morris (1972), Perrin (1982) and Dippenaar & Rautenbach (1986), led to the recognition of seven tooth-wear classes (Figure 1).

A basic set of 11 linear cranial measurements (5 skull, 3 mandible and 3 dental) was recorded by one of us (CTC) to the nearest 0,05 mm using Mitutoyo digital callipers and DataQ (D.L. Schultz) for direct data input into Quattro (Borland International Inc.). In addition, four descriptive characters (breadth of brain-case, least breadth of interorbital constriction, greatest bulla length and greatest height of skull) were taken. The measurements are defined and illustrated in Figure 2.

After data screening, which resulted in the exclusion of one outlier from Boekenhoutkloof (TM 30432), the four samples were independently subjected to Model I two-way analysis of variance (ANOVA). From the ANOVA tables, estimates of % *SSQ* of four sources of variation (sex, age, sex-age interaction and error (= residual)) were computed by the division of the *SSQ* associated with each source of variation by the total *SSQ*. Analysis also included *a posteriori* Student-Newman-Keuls (SNK) tests for maximally non-significant subsets ($P < 0{,}05$; Sokal & Rohlf 1969; 1981). Haldane's (1955) correction was used in the computation of coefficients of variation (CV).

All univariate analyses were based on the 11 basic and four descriptive characters. The material available was

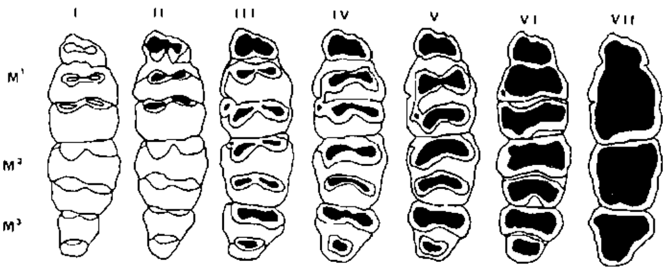

Figure 1 Right maxillary tooth-row of *Aethomys namaquensis* illustrating seven tooth-wear classes. Tooth-wear class I: cheek-teeth not fully erupted, M^3 conspicuously below eruption level of M^1 and M^2 (TM 27832); tooth-wear class II: cheek-teeth fully erupted, M^3 somewhat smaller, cusps conspicuous but with no or very little wear (TM 27842); tooth-wear class III: all cheek-teeth in apposition, minimal cusp wear (TM 31258); tooth-wear class IV: cusp wear obvious, but not extensive (TM 30433); tooth-wear class V: cusp wear extensive, but most cusps still distinguishable (TM 30432); tooth-wear class VI: cusp wear extensive, but traces of cusps not completely lost (TM 30438); tooth-wear class VII: tooth-wear severe, occlusal surfaces worn smooth with no traces of cusps (TM 30428).

characterized by small sample sizes, particularly of tooth-wear classes I and VII, so that not all (and in some cases not consecutive) tooth-wear classes were represented. This led to univariate analyses based on either *three* (Narap: tooth-wear classes II, III and VI; Olifantspoort: II, III and IV, and Al-te-ver: III, IV and V) or *four* (Boekenhoutkloof: III, IV, V, VI) tooth-wear classes.

Variation due to sex and age was also examined by principal component (PCA) (Thorpe 1980; Gould 1984; James & McCulloch 1990) and cluster analyses (Sneath & Sokal 1973) based on standardized characters. PCA was computed from a correlation matrix while unweighted pair-group arithmetic average cluster analysis (UPGMA) was based on average taxonomic distances (Rohlf 1986; Sneath & Sokal 1973). Unlike univariate analysis, PCA and UPGMA allowed the analysis of a wider range of tooth-wear classes that also included the poorly represented tooth-wear classes I and VII. Canonical variates analyses (CVA) (Pimentel & Smith 1986b) of tooth-wear classes (excluding those with too few observations) were also undertaken. Multivariate analysis of variance (MANOVA) was used to test for significant differences between group centroids. All multivariate analyses were based on the basic set of 11 cranial measurements.

Statistical analyses were undertaken with BIOΣTAT I and II (Pimentel & Smith 1986a; 1986b) and NTSYS-pc (Rohlf 1986).

Univariate assessment

Univariate results for the four samples analysed were broadly congruent for the 11 basic and four descriptive measurements and, therefore, predominantly the results for *A. namaquensis* from Boekenhoutkloof and *A. chrysophilus* from Olifantspoort are presented. The former sample was the largest individual sample and also included the widest range of consecutive tooth-wear classes (III – VI), whereas

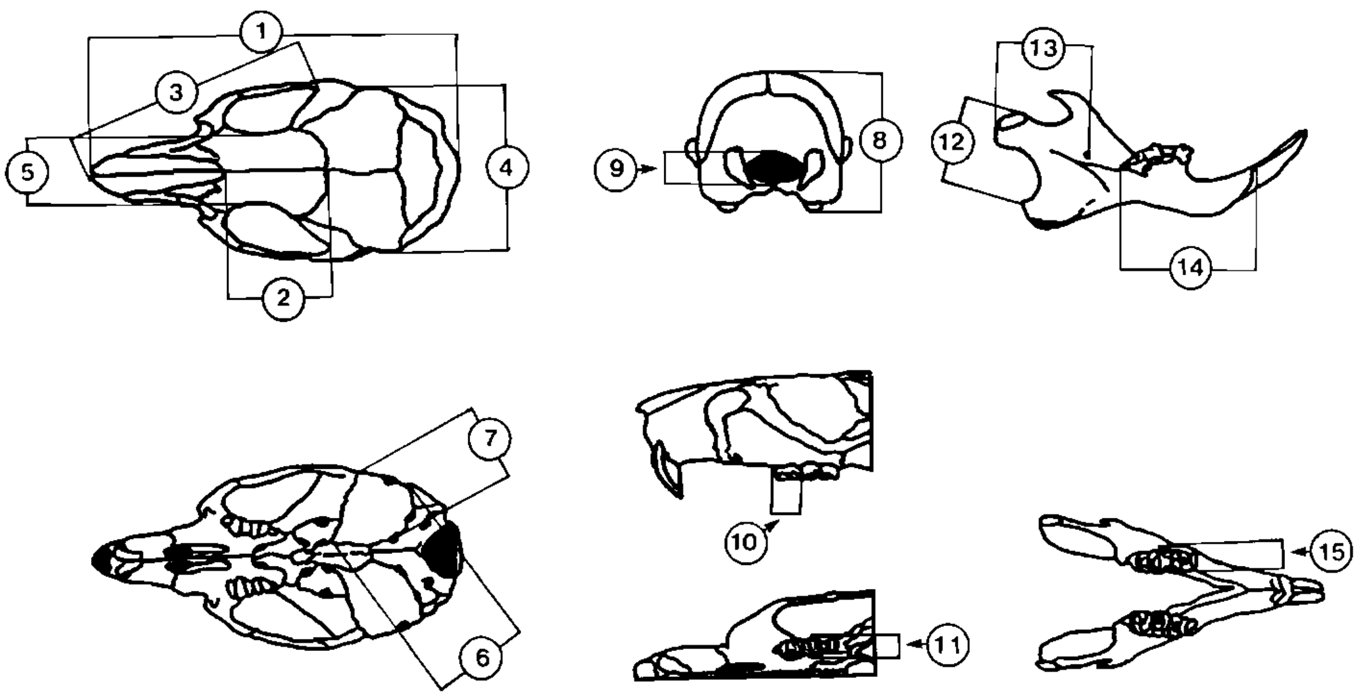

Figure 2 Abbreviations and reference points of skull measurements: 1. GLS: greatest length of skull, from anterior edge of nasals to posterior margins of the skull, along longitudinal axis; 2. FRO: greatest length of frontals; 3. NPP: distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch; 4. BBC: breadth of brain-case – width at dorsal root of squamosals; 5. IOB: least breadth of interorbital constriction – least distance dorsally between orbits; 6. BUL: greatest bulla length at 45° angle to skull axis; 7. BUW: greatest bulla width at 45° angle to skull axis; 8. GHS: greatest height of skull perpendicular to horizontal plane through bullae; 9. FMH: foramen magnum height – widest part of foramen in vertical plane; 10. LFM: length of M^1 along cingulum; 11. WSM: greatest cross-sectional crown width of M^2; 12. AFA: angular process – mandibular condyle length, in straight line from ventral edge of angular process to mid-dorsal ridge of mandibular condyle; 13. MAF: mandibular foramen – mandibular condyle length, from ventral edge of mandibular foramen to mid-posterodorsal edge of mandibular condyle; 14. IML: posterior incisor – M_3 length, in a straight line from posterior edge of I_1 alveolus to posterior edge of M_3 alveolus; 15. WMS: greatest cross-sectional crown width of M_2.

the latter sample included tooth-wear classes II – IV. *F*-values from Model I two-way ANOVA and % *SSQ* for the two samples (Table 1) show that more measurements have significant ($P < 0{,}01$) *F*-values for age than for sex in both samples. Similarly, age generally gave higher % *SSQ* values (range % *SSQ* = 1,57–45,56 for *A. namaquensis*; 7,41–83,59 for *A. chrysophilus*) than sex (0,00–9,99 for *A. namaquensis*; 0,05–40,00 for *A. chrysophilus*). Distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch (NPP), angular process – mandibular condyle length (AFA) and mandibular foramen – mandibular condyle length (MAF) showed significant age variation in both samples. The importance of these measurements was also apparent in the *A. namaquensis* sample from Narap and the *A. chrysophilus* sample from Al-te-ver. Generally, these measurements also contributed relatively more to the total variance due to age.

Only one measurement, least breadth of interorbital constriction (IOB) in the Boekenhoutkloof sample, and two measurements, greatest height of skull (GHS) and greatest cross-sectional crown width of M^2 (WSM) in the *A. chrysophilus* sample from Olifantspoort, showed significant sexual dimorphism. These measurements also showed the largest per cent contribution to the total variance due to sex (Table 1).

Only one measurement from each sample (distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch (NPP) and greatest cross-sectional crown width of M_2 (WMS)) showed significant interaction between age and sex. The negligible contribution due to sex-age interaction was also shown by the relatively small % *SSQ* means in both samples (mean % *SSQ* = 6,39 in *A. namaquensis*; 10,67 in *A. chrysophilus*). In both samples, the largest per cent contribution to the total variance was due to error (mean % *SSQ* = 79,54; range % *SSQ* = 44,11–92,00 in *A. namaquensis*; 45,45, 14,07–73,65 in *A. chrysophilus*).

Despite the congruence of univariate results among the four samples, % *SSQ* contributions generally showed a much higher degree of congruence between 'three tooth-wear class'-group analyses in samples of *A. chrysophilus* from Olifantspoort (mean % *SSQ* contributions for sex = 7,48; age = 36,40; interaction = 10,67; error = 45,45) and Al-te-ver (sex = 8,75; age = 32,76; interaction = 13,43; error = 45,06), and *A. namaquensis* from Farm Narap (sex = 2,70; age 43,42; interaction = 7,23; error = 46,65) than the 'four tooth-wear class'-group analysis in the *A. namaquensis* sample from Boekenhoutkloof (sex = 1,71; age = 12,36; interaction = 6,39; error = 79,54). In addition, except for the error component, the 'three tooth-wear class'-group analyses showed higher % *SSQ* values than the 'four tooth-wear class'-group analysis.

In the SNK tests, a large number of measurements in all samples showed no significant differences between tooth-wear classes analysed: Boekenhoutkloof (10; classes III –

Table 1 *F*-values and % Sum of Squares (% *SSQ*) of each source of variation from a Model I two-way ANOVA of (a) four tooth-wear classes (III – VI) of male and female *Aethomys namaquensis* from Boekenhoutkloof and (b) three tooth-wear classes (II – IV) of male and female *Aethomys chrysophilus* from Olifantspoort. Statistical significance: * = $P < 0{,}05$; ** = $P < 0{,}01$; *** = $P < 0{,}001$. Measurements are defined in Figure 2

Measure-ment	*F*-value			% *SSQ*			
	Sex(S)	Age(A)	S × A	Sex(S)	Age(A)	S × A	Error
(a) Boekenhoutkloof							
GLS	1,26	0,56	0,31	3,00	4,04	2,23	90,73
FRO	0,96	0,75	0,13	2,31	5,40	0,94	91,35
NPP	0,49	13,08***	2,80*	0,57	45,56	9,76	44,11
BBC	0,00	0,66	1,52	0,00	4,43	10,26	85,31
IOB	6,07*	2,87*	2,71	9,99	14,14	13,41	62,46
BUL	0,52	0,40	1,13	1,21	2,79	7,86	88,14
BUW	0,25	1,07	0,20	0,59	7,59	1,42	90,40
GHS	0,05	1,15	1,02	0,11	7,76	6,86	85,27
FMH	0,90	0,22	0,92	2,10	1,57	6,54	89,79
LFM	0,45	1,59	1,94	0,94	9,74	11,85	77,47
WSM	0,07	0,68	1,84	0,00	4,71	12,04	83,25
AFA	0,03	5,04**	0,80	0,05	27,22	4,33	68,40
MAF	0,15	4,21**	0,34	0,30	24,39	1,96	73,35
IML	2,02	3,50*	0,99	3,78	19,61	5,55	71,06
WMS	0,24	0,88	0,06	0,80	6,40	0,80	92,00
Mean				1,71	12,36	6,39	79,54
(b) Olifantspoort							
GLS	0,52	11,21**	0,43	1,44	62,62	2,41	33,53
FRO	0,14	6,03*	1,24	0,53	45,21	9,32	44,94
NPP	0,95	5,04*	2,88	3,23	36,60	19,52	40,65
BBC	0,21	6,17**	0,49	0,82	48,31	3,86	47,01
IOB	2,22	2,00	0,45	11,57	21,00	4,71	62,72
BUL	1,48	35,66***	0,26	1,73	83,59	0,61	14,07
BUW	0,06	1,40	0,72	0,33	17,18	8,84	73,65
GHS	7,95**	1,37	1,92	29,97	10,33	14,49	45,21
FMH	2,30	1,82	0,05	12,79	20,23	0,57	66,41
LFM	1,00	1,57	2,13	4,68	15,21	21,05	59,06
WSM	11,26**	1,76	0,69	40,00	12,31	4,62	43,07
AFA	0,02	18,35***	2,11	0,05	69,33	7,96	22,66
MAF	0,50	12,96***	0,57	1,25	65,53	2,90	30,32
IML	0,02	3,05	0,71	0,11	31,18	7,32	61,39
WMS	1,38	1,07	8,50**	3,70	7,41	51,85	37,04
Mean				7,48	36,40	10,67	45,45

VI), Narap (6; II, III, VI), Olifantspoort (6; II – IV), and Al-te-ver (8; III – V), the highest numbers being recorded in the first and last samples which included only tooth-wear class III and older individuals. (Representative results for the four samples are presented in Table 2.) Conversely, in the samples that included tooth-wear class II and older individuals (Olifantspoort and Narap), most measurements (9 of 15 in each sample) showed significant variation between tooth-wear classes. In instances in which significance was recorded, either all tooth-wear classes differed significantly in a few measurements (Olifantspoort and Narap three measurements, Al-te-ver four), or were variously grouped into non-significant subsets: in *A. namaquensis* from 1) Boekenhoutkloof (which represented the widest range of consecutive tooth-wear classes) classes V and VI were mostly grouped in non-significant subsets, and sometimes IV and VI, and III and IV; and from 2) Narap, tooth-wear classes II and III were consistently grouped into the same non-significant subset, with both differing significantly from tooth-wear class VI. In *A. chrysophilus* from both Olifantspoort and Al-te-ver, tooth-wear classes III and IV were consistently grouped in the same non-significant subset. The pattern that emerges from the SNK analyses is that the inclusion of tooth-wear class II individuals with tooth-wear class III and older individuals leads to an increase in the number of measurements showing significant age variation, and that analysis of only tooth-wear class III and older specimens also show a large proportion of measurements with significant differences; tooth-wear class III individuals either fall in the same non-significant subset as those of either tooth-wear class II or tooth-wear class IV. The SNK results therefore suggest that individuals of tooth-wear classes II and III should be excluded from the final data set, and that an argument could even be made for the exclusion of tooth-wear class IV individuals.

Descriptive statistics of all samples show a direct relationship between character magnitude and age, as exemplified by samples from Boekenhoutkloof and Olifantspoort (Table 3).

Multivariate assessment

The multivariate assessment focuses on the relatively large samples of *A. namaquensis* from Boekenhoutkloof and Narap, with reference to the samples of *A. chrysophilus* from Olifantspoort and Al-te-ver. The Narap sample is of particular interest in the multivariate analyses since it includes individuals representing all seven tooth-wear classes. Because of insufficient cell sizes for a combined CVA of males, females and tooth-wear classes, the data were first subjected to principal component and cluster analyses.

The first two principal components from analyses of the Boekenhoutkloof and Narap samples are shown in Figure 3. Both scattergrams reflect age rather than sex as the major source of variation in both samples. Tooth-wear class III individuals from Boekenhoutkloof tend to separate from those of tooth-wear classes IV – VII at an oblique angle. There is no clear separation between tooth-wear classes IV – VII along either axis. In the PCA of the Narap sample, there is clear separation between tooth-wear classes IV – VII and tooth-wear classes I – III, especially along the first axis. An examination of the remaining axes (3 – 14) for both samples did not reveal any separation of tooth-wear classes. In both samples, the first principal component generally had high and negative loadings on most measurements (Table 4), with generally high per cent variances associated with each measurement's component contribution (in parentheses in Table 4). The important measurements with relatively high loadings on the first axis (35,4% of the total variance) in the Boekenhoutkloof sample (Table 4a) are: greatest length of skull (GLS), distance from anterior edge of nasals to

Table 2 Multiple range SNK tests of tooth-wear classes in *Aethomys namaquensis* from (a) Boekenhoutkloof (tooth-wear classes III – VI) and (b) Narap (II, III and VI), and *Aethomys chrysophilus* from (c) Olifantspoort (II – IV) and (d) Al-te-ver (III – V). Non-significant subsets ($P < 0,05$) are indicated by vertical lines; NS = no significant differences; AS = all means significantly different; n = sample size; SD = standard deviation. Measurements are defined in Figure 2

Measurement	Tooth-wear class (n)	SD	Mean		Measurement	Tooth-wear class (n)	SD	Mean	
(a) Boekenhoutkloof									
GLS	III(5)	0,66	28,78		NPP	III(5)	0,56	20,34	
	VI(11)	0,80	29,57	NS		V(17)	0,66	21,48	
	IV(17)	0,45	29,87			V(13)	0,65	22,01	
	V(13)	0,68	30,28			VI(11)	0,68	22,27	
AFA	III(5)	0,48	5,58		IML	III(5)	0,29	8,56	
	IV(17)	0,33	6,07			V(13)	0,21	8,81	
	V(13)	0,34	6,13			IV(17)	0,30	8,78	
	VI(11)	0,18	6,23			VI(11)	0,29	9,01	
(b) Narap									
GLS	II(4)	0,93	27,19		BBC	II(4)	0,26	12,39	
	III(11)	0,69	28,36	AS		III(11)	0,30	12,73	
	VI(5)	0,93	31,80			VI(5)	0,35	13,25	
BUW	II(4)	0,10	4,73		WMS	II(4)	0,05	1,67	
	III(11)	0,19	4,89			III(11)	0,04	1,67	NS
	VI(5)	0,16	5,16			VI(5)	0,04	1,69	
(c) Olifantspoort									
FRO	II(4)	0,38	9,71		BUL	II(4)	0,07	6,71	
	III(10)	0,48	10,31			III(10)	0,14	7,24	AS
	IV(4)	0,18	10,84			IV(4)	0,03	7,41	
FMH	II(4)	0,14	4,59		MAF	II(4)	0,17	3,89	
	III(10)	0,16	4,64	NS		III(10)	0,31	4,69	
	IV(4)	0,19	4,80			IV(4)	0,23	4,81	
(d) Al-te-ver									
BBC	III(8)	0,30	14,03		IOB	III(8)	0,14	4,83	
	IV(7)	0,61	14,31			IV(7)	0,32	4,88	NS
	V(5)	0,46	14,89			V(5)	0,22	5,08	
LFM	IV(7)	0,12	2,80		AFA	III(8)	0,24	6,44	
	III(8)	0,11	2,83			IV(7)	0,30	6,87	AS
	V(5)	0,09	2,98			V(5)	0,45	7,51	

anterior edge of posterior part of zygomatic arch (NPP), angular process – mandibular condyle length (AFA), mandibular foramen – mandibular condyle length (MAF) and posterior incisor – M_3 length (IML). In addition to these measurements, greatest length of frontals (FRO), greatest bulla width (BUW) and greatest cross-sectional crown width of M_2 (WMS) are important on the first axis (64,9%) of the Narap sample (Table 4b). Important measurements on the second axis (16,1%) of the Boekenhoutkloof sample are: greatest length of frontals (FRO), greatest cross-sectional crown widths of M^2 (WSM) and M_2 (WMS) (Table 4a). In the Narap sample, foramen magnum height (FMH) was important on the second axis (11,5%) (Table 4b). Collectively, most of these measurements also feature either as significantly different or contribute highly towards the total *% SSQ*s in the univariate statistics. Results for *A. chrysophilus* from Olifantspoort reflected those for the Boekenhoutkloof sample in that there was some overlap between tooth-wear classes III and IV, but in the *A. chrysophilus* sample from Al-te-ver, the overlap was greater. However, both these samples included tooth-wear class II individuals (and in the case of Al-te-ver a single tooth-wear class I individual) and their positions in the PCA graphs closely reflected the pattern observed in the Narap sample. In all PCA graphs there was little, if any, indication of sexual dimorphism.

Because of the relatively low level of variation explained by successive components (e.g. first three axes for *A. namaquensis:* Boekenhoutkloof (62,3%), Narap (86,3%); *A. chrysophilus:* Al-te-ver (84,5%), Olifantspoort (76,4%)), the samples were also examined by cluster analyses. In the Boekenhoutkloof sample, the phenogram showed no discrete

Table 3 Standard statistics of 15 measurements of males and females in (a) five tooth-wear classes of *Aethomys namaquensis* from Boekenhoutkloof and (b) three tooth-wear classes of *Aethomys chrysophilus* from Olifantspoort. $\bar{Y}$ = arithmetic mean; $2SE$ = two standard errors; CV = coefficient of variation; n = sample size. Measurements are defined in Figure 2

(a) Boekenhoutkloof

Sex	Tooth-wear class (n)		Measurement							
			GLS	FRO	NPP	BBC	IOB	BUL	BUW	GHS
Males	III (3)	$\bar{Y}$	28,44	9,35	20,08	12,72	4,36	6,47	4,78	9,60
		$2SE$	0,26	0,16	0,26	0,17	0,04	0,21	0,21	0,22
		CV	1,61	2,90	2,27	2,27	1,53	5,62	7,55	3,91
	IV (8)	$\bar{Y}$	29,40	9,49	21,12	13,19	4,67	6,57	4,87	9,78
		$2SE$	0,31	0,22	0,29	0,16	0,10	0,13	0,09	0,05
		CV	3,02	6,44	3,86	3,40	5,86	5,51	5,30	1,44
	V (7)	$\bar{Y}$	30,40	9,68	22,05	12,92	4,49	6,57	4,85	9,75
		$2SE$	0,24	0,12	0,23	0,12	0,03	0,07	0,10	0,10
		CV	2,26	3,59	2,96	2,71	1,78	3,20	5,75	2,82
	VI (6)	$\bar{Y}$	31,37	9,79	22,54	13,03	4,75	6,80	4,92	9,78
		$2SE$	0,10	0,13	0,10	0,16	0,04	0,08	0,04	0,08
		CV	0,77	3,36	1,05	2,96	2,29	2,78	1,81	1,99
Females	III (2)	$\bar{Y}$	29,28	9,36	20,73	13,32	4,52	6,55	4,68	9,75
		$2SE$	0,49	0,03	0,42	0,08	0,05	0,06	0,01	0,06
		CV	2,37	0,46	2,83	0,80	1,56	1,30	0,30	0,80
	IV (9)	$\bar{Y}$	30,29	9,42	21,80	13,01	4,44	6,62	4,92	9,86
		$2SE$	0,14	0,20	0,08	0,12	0,05	0,08	0,04	0,08
		CV	1,40	6,29	1,06	2,77	3,09	3,64	2,45	2,56
	V (5)	$\bar{Y}$	30,28	9,40	21,94	12,92	4,48	6,51	4,88	9,54
		$2SE$	0,32	0,29	0,32	0,12	0,08	0,15	0,06	0,08
		CV	2,35	6,78	3,21	2,04	4,07	5,04	2,66	1,98
	VI (5)	$\bar{Y}$	30,54	9,60	21,95	13,00	4,53	6,47	4,94	9,68
		$2SE$	0,48	0,33	0,41	0,10	0,07	0,16	0,04	0,18
		CV	3,53	7,67	4,17	1,72	3,49	5,41	1,77	4,22
	VII (2)	$\bar{Y}$	31,17	9,46	22,53	13,01	4,98	6,91	4,90	9,86
		$2SE$	0,30	0,21	0,20	0,50	0,16	0,02	0,13	0,06
		CV	1,34	3,07	1,22	5,44	4,41	0,41	3,75	0,86

Sex	Tooth-wear class (n)		FMH	LFM	WSM	AFA	MAF	IML	WMS
Males	III (3)	$\bar{Y}$	4,56	2,23	1,82	5,44	4,25	8,41	1,68
		$2SE$	0,13	0,16	0,03	0,10	0,06	0,15	0,03
		CV	4,94	12,63	2,77	3,11	2,27	3,14	3,09
	IV (8)	$\bar{Y}$	4,53	2,49	1,76	6,12	4,51	8,72	1,67
		$2SE$	0,08	0,03	0,02	0,09	0,08	0,08	0,02
		CV	4,78	3,53	2,87	4,30	4,82	2,50	3,42
	V (7)	$\bar{Y}$	4,46	2,56	1,80	6,10	4,59	8,81	1,65
		$2SE$	0,06	0,08	0,04	0,11	0,12	0,13	0,01
		CV	3,93	8,78	5,24	5,26	7,16	4,06	2,40
	VI (6)	$\bar{Y}$	4,49	2,53	1,74	6,33	4,71	8,99	1,68
		$2SE$	0,08	0,03	0,02	0,08	0,07	0,12	0,03
		CV	4,55	2,82	3,00	3,05	3,42	3,13	4,82
Females	III (2)	$\bar{Y}$	4,34	2,47	1,80	5,78	4,11	8,79	1,69
		$2SE$	0,03	0,08	0,04	0,60	0,35	0,12	0,04
		CV	0,98	4,58	2,76	14,68	11,89	1,93	2,94
	IV (9)	$\bar{Y}$	4,45	2,48	1,79	6,02	4,61	8,90	1,66
		$2SE$	0,61	0,07	0,02	0,13	0,07	0,06	0,02
		CV	4,12	8,02	3,50	6,53	4,53	2,05	3,16
	V (5)	$\bar{Y}$	4,55	2,38	1,74	6,17	4,54	8,75	1,63
		$2SE$	0,08	0,06	0,02	0,18	0,18	0,08	0,01
		CV	4,08	5,30	3,10	6,67	8,94	2,16	1,76

Table 3 Continued

(a) Boekenhoutkloof

Sex	Tooth-wear class (*n*)		FMH	LFM	WSM	AFA	MAF	IML	WMS
	VI (5)	$\bar{Y}$	4,38	2,48	1,79	6,17	4,79	9,03	1,67
		2*SE*	0,07	0,02	0,02	0,05	0,19	0,15	0,03
		CV	3,79	2,07	2,55	1,83	8,75	3,72	3,74
	VII (2)	$\bar{Y}$	4,55	2,62	1,83	6,71	5,02	8,99	1,67
		2*SE*	0,16	0,21	0,01	0,25	0,11	0,08	0,09
		CV	4,82	11,34	0,77	5,27	3,10	1,18	7,22

(b) Olifantspoort

Sex	Tooth-wear class (*n*)		GLS	FRO	NPP	BBC	IOB	BUL	BUW	GHS
Males	II (2)	$\bar{Y}$	31,00	9,72	22,12	13,15	4,70	6,74	5,15	11,22
		2*SE*	0,95	0,13	0,09	0,24	0,07	0,07	0,11	0,11
		CV	4,31	1,88	1,43	2,53	1,96	1,47	2,89	1,32
	III (7)	$\bar{Y}$	33,68	10,42	23,54	13,88	4,90	7,25	5,45	11,33
		2*SE*	0,43	0,15	0,39	0,09	0,09	0,06	0,05	0,12
		CV	3,39	3,68	4,38	1,78	4,64	2,25	2,32	2,74
	IV (2)	$\bar{Y}$	33,87	10,58	23,73	13,99	4,84	7,41	5,38	10,98
		2*SE*	0,46	0,36	0,31	0,44	0,01	0,02	0,01	0,20
		CV	1,92	4,81	1,82	4,40	0,15	0,38	0,13	2,51
Females	II (2)	$\bar{Y}$	30,97	9,67	21,56	13,32	4,55	6,69	5,33	10,64
		2*SE*	0,08	0,45	0,03	0,32	0,07	0,03	0,06	0,29
		CV	0,37	6,51	0,16	3,40	2,02	0,63	1,46	3,79
	III (3)	$\bar{Y}$	33,14	10,06	23,30	13,69	4,71	7,20	5,36	10,86
		2*SE*	0,41	0,40	0,42	0,22	0,15	0,04	0,22	0,15
		CV	2,14	6,84	3,15	2,83	5,45	1,06	7,00	2,31
	IV (2)	$\bar{Y}$	34,36	11,10	24,42	14,06	4,86	7,41	5,40	11,07
		2*SE*	0,92	0,08	0,92	0,10	0,06	0,03	0,15	0,04
		CV	3,77	1,02	5,30	1,01	1,75	0,57	3,93	0,51

Sex	Tooth-wear class (*n*)		FMH	LFM	WSM	AFA	MAF	IML	WMS
Males	II (2)	$\bar{Y}$	4,74	2,67	1,85	5,55	4,03	9,13	1,80
		2*SE*	0,20	0,02	0,04	0,22	0,05	0,27	0,03
		CV	5,97	0,80	3,06	5,61	1,58	4,18	2,36
	III (7)	$\bar{Y}$	4,60	2,59	1,85	6,60	4,67	9,86	1,68
		2*SE*	0,06	0,03	0,02	0,12	0,13	0,15	0,02
		CV	3,67	3,49	2,68	4,81	7,62	4,10	2,62
	IV (2)	$\bar{Y}$	4,53	2,67	1,91	6,62	4,81	9,82	1,75
		2*SE*	0,10	0,04	0,05	0,22	0,19	0,38	0,01
		CV	2,97	2,12	3,70	4,60	5,59	5,40	0,41
Females	II (2)	$\bar{Y}$	4,86	2,45	1,75	5,82	3,76	9,52	1,65
		2*SE*	0,09	0,03	0,04	0,19	0,08	0,02	0,04
		CV	2,62	1,73	2,84	4,50	3,01	0,22	3,43
	III (3)	$\bar{Y}$	4,72	2,59	1,80	6,37	4,74	9,86	1,72
		2*SE*	0,08	0,08	0,01	0,11	0,12	0,10	0,02
		CV	2,85	5,14	0,85	3,03	4,19	1,71	2,42
	IV (2)	$\bar{Y}$	4,65	2,67	1,81	7,00	4,81	9,64	1,68
		2*SE*	0,12	0,08	0,03	0,06	0,21	0,29	0,01
		CV	3,50	3,98	2,34	1,11	6,17	4,18	0,42

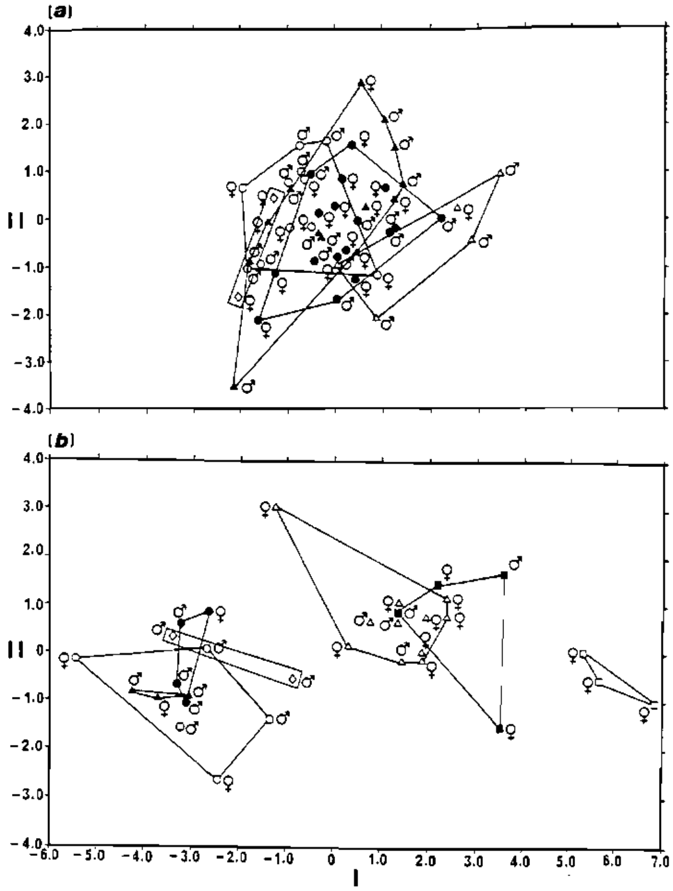

Figure 3 The first two axes from principal component analyses of *Aethomys namaquensis* from (a) Boekenhoutkloof and (b) Narap. The sex and tooth-wear classes [I (□); II (■); III (△); IV (●); V (▲); VI (○); VII (◇)] of all individuals are indicated. Minimum convex polygons enclose individuals of each tooth-wear class.

groupings of either sexes or tooth-wear classes, except for three individuals of tooth-wear class III and one individual each of tooth-wear classes IV and V which seem to form a subcluster in accordance with PCA results (Figure 4a). In the Narap sample, two major clusters were apparent: one comprising all individuals of tooth-wear classes I – III, with a subcluster comprising all individuals of tooth-wear class I (except for one individual of tooth-wear class II), and the other comprising all individuals of tooth-wear classes IV – VII (except for one individual of tooth-wear class III) (Figure 4b). Both samples showed no discrete groupings of sexes. Similar patterns were evident in the *A. chrysophilus* samples from Olifantspoort and Al-te-ver (cophenetic correlation coefficients = 0,69 and 0,83, respectively) in that tooth-wear class I and II individuals formed distinct subclusters, but as in the PCA results, the distinction between tooth-wear classes III and IV – VII were not as marked as in the Narap sample.

MANOVA of males and females, for which specimens of the tooth-wear classes indicated below had to be pooled to increase cell sizes, indicated no significant sexual differences in any of the samples (Boekenhoutkloof, classes IV – VI: F = 0,63; P > 0,05; Olifantspoort IV – VI: F = 0,97; P > 0,05; Narap IV – VI: F = 0,66; P > 0,05; Al-te-ver IV and V: F = 1,69; P > 0,05). These results, together with the univariate results, led us to pool the sexes for discriminant analyses of tooth-wear classes.

Results of discriminant analyses are exemplified by a 'four tooth-wear class (III – VI) analysis of the relatively large individual sample from Boekenhoutkloof (Figure 5). It produced a 71,0% overall *a posteriori* classification, and in the scattergram of canonical variates I and II, four of five tooth-wear class III individuals tend to plot apart from individuals of tooth-wear classes IV – VI along the first canonical variate (54,9% variance). Individuals of tooth-wear class III are maximally separated from individuals of tooth-wear class V along the second axis (38,9%). Except for the greatest length of frontals (FRO), greatest bulla width (BUW) and greatest cross-sectional crown width of M_2 (WMS), which loaded highly in the PCA's first axis of the Narap sample, all measurements that load highly in the PCA of the Boekenhoutkloof and Narap samples also load highly in the CVA (Table 5). The posterior incisor – M_3 length (IML), together with greatest cross-sectional crown

Table 4 Loadings of measurements on the first two components from principal component analyses of *Aethomys namaquensis* from (a) Boekenhoutkloof and (b) Narap. The per cent variance contribution is given in parentheses. Measurements are defined in Figure 2

Measurement	Principal component axes I	Principal component axes II
(a) Boekenhoutkloof		
GLS	−0,882 (77,75)	0,298 (8,86)
FRO	−0,139 (1,94)	0,563 (31,67)
NPP	−0,890 (79,18)	0,355 (12,63)
BUW	−0,379 (14,35)	−0,269 (7,26)
FMH	0,067 (0,44)	−0,493 (24,31)
LFM	−0,493 (24,26)	−0,288 (8,27)
WSM	0,188 (3,53)	−0,654 (42,72)
AFA	−0,749 (56,04)	−0,011 (0,01)
MAF	−0,814 (66,31)	0,145 (2,11)
IML	−0,768 (59,05)	−0,295 (8,70)
WMS	−0,256 (6,54)	−0,551 (30,38)
% trace:	Axis I = 35,4%;	Axis II = 16,1%
(b) Narap		
GLS	−0,977 (95,42)	−0,058 (0,33)
FRO	−0,772 (59,57)	−0,281 (7,91)
NPP	−0,974 (94,81)	−0,071 (0,51)
BUW	−0,909 (82,65)	0,120 (1,43)
FMH	−0,188 (3,52)	0,781 (60,94)
LFM	−0,618 (38,21)	0,088 (0,78)
WSM	−0,642 (41,27)	0,368 (13,56)
AFA	−0,939 (88,15)	−0,208 (4,31)
MAF	−0,903 (81,61)	−0,206 (4,23)
IML	−0,887 (78,71)	−0,218 (4,77)
WMS	−0,708 (50,15)	0,525 (27,52)
% trace:	Axis I = 64,9%;	Axis II = 11,5%

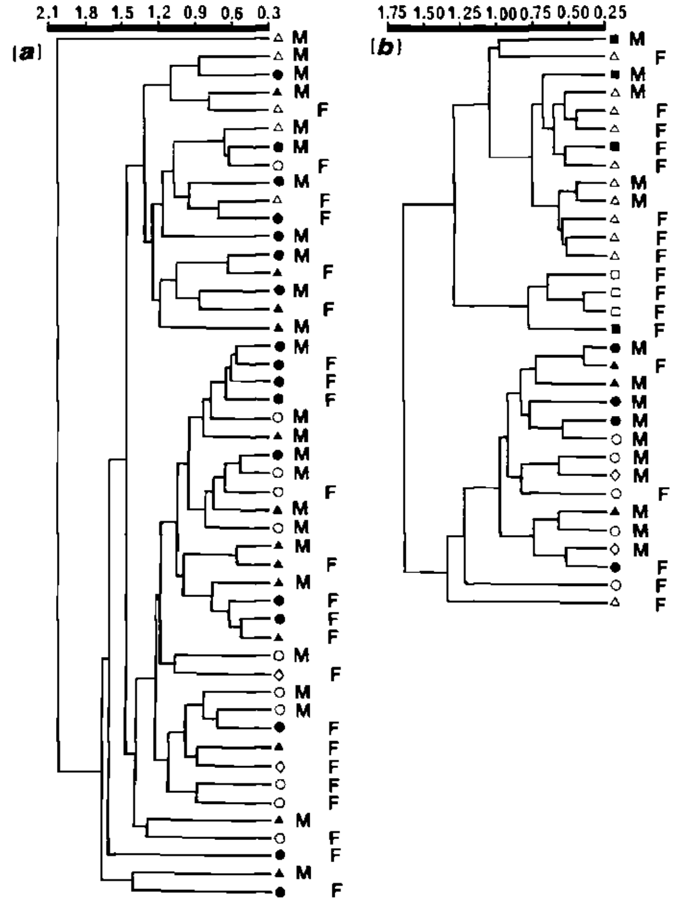

Figure 4 Distance phenograms from UPGMA cluster analyses of *Aethomymys namaquensis* from (a) Boekenhoutkloof and (b) Narap. The sex (M = males; F = females) and tooth-wear classes [I (□); II (■); III (△); IV (●); V (▲); VI (○); VII (◇)] of all individuals are indicated. Cophenetic correlation coefficients = 0,66 and 0,73, respectively.

Table 5 Loadings of measurements on the first two axes from a canonical variates analysis of *Aethomys namaquensis* from Boekenhoutkloof. The per cent variance contribution is given in parentheses. Measurements are defined in Figure 2

	Canonical variates axes	
Measurement	I	II
GLS	0,787 (1,97)	–0,180 (85,13)
FRO	0,211 (59,29)	–0,010 (39,69)
NPP	0,824 (3,47)	0,023 (95,77)
BUW	0,218 (12,48)	–0,208 (1,87)
FMH	–0,048 (9,72)	0,078 (89,16)
LFM	0,281 (13,75)	0,039 (76,91)
WSM	–0,264 (84,81)	–0,069 (14,57)
AFA	0,549 (87,06)	–0,084 (10,39)
MAF	0,497 (2,63)	–0,152 (80,11)
IML	0,409 (1,48)	–0,365 (95,80)
WMS	–0,113 (93,16)	–0,315 (0,23)
% trace:	Axis I = 54,9%;	Axis II = 38,9%

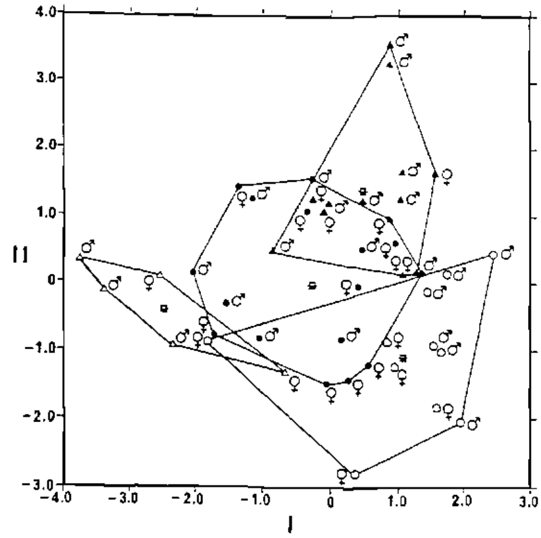

Figure 5 The first two axes from a canonical variates analysis of tooth-wear classes in *Aethomys namaquensis* from Boekenhoutkloof. The tooth-wear classes [III (△); IV (●); V (▲); VI (○)] and sex of all individuals are indicated. Minimum convex polygons enclose individuals of each tooth-wear class. Group centroids are denoted by (✱).

width of M_2 (WMS) are the important measurements on the second canonical variate. MANOVA indicated significant differences between the group centroids of the four tooth-wear classes (F = 1,91; P = 0,01). Except for the Olifantspoort sample that indicated no significant differences between group centroids of the analysed tooth-wear classes (II – IV) (F = 1,76; P = 0,18), the remaining two samples indicated significant differences between group centroids (Narap: F = 2,56; P = 0,01, tooth-wear classes II – IV and VI; Al-te-ver: F = 2.53; P = 0,04, tooth-wear classes III – V).

Discussion and Conclusions

The primary objective of this study was to examine age- and sex-related morphometric variation in *Aethomys* with a view to ascertaining 1) whether the sexes should be treated separately or together, and 2) which subset(s) of tooth-wear classes represent specimens that have reached adult dimensions and therefore are eligible for inclusion in subsequent morphometric studies of the genus.

Both univariate and multivariate results clearly showed a lack of sexual dimorphism in the two species studied. However, with regard to age variation, the univariate SNK tests did not provide unequivocal results as to which tooth-wear classes to consider in subsequent studies. This is resolved when the univariate and multivariate results are interpreted together, showing that there is an increase in dimensions as one progresses from tooth-wear class I to at least IV. The SNK results suggest that individuals of tooth-wear classes II and III should be excluded from the final data set, and that an argument could even be made for the exclusion of tooth-wear class IV individuals. In the principal component analyses both tooth-wear classes I and II, and in two instances, tooth-wear class III as well, plotted well apart from the other tooth-wear classes. In two other instances, there was some to extensive overlap between tooth-wear class III and some of the higher tooth-wear classes.

With regard to only tooth-wear classes IV – VII, in some of the SNK tests the first tooth-wear class appeared in the same non-significant subset as tooth-wear class III. However, in the principal component analyses, and in the discriminant analysis of the largest sample from Boekenhoutkloof, specimens of tooth-wear classes IV – VII plot close together.

If the tooth-wear classes are visualized as demarcating sections of variable and unknown length on a hypothetical growth curve, then individuals of tooth-wear class III seem to fall at a point on the curve just before it begins to stabilize, and our results provide justification for pooling tooth-wear classes IV – VI for subsequent recording and analyses in the systematic revision of the genus. Tooth-wear class VII individuals are excluded from the final data set because, 1) very few individuals of this tooth-wear class are encountered in collections, 2) extensive tooth-wear often renders measuring points on the teeth uncertain, and 3) there seems to be a higher incidence of age-related deformations in very old rodents in general (N.J. Dippenaar, pers. obs.).

The univariate *% SSQ* analysis of the four samples indicated that most measurements have relatively small sex and age components but a large error component. Similar patterns were observed in six of the seven species examined by Straney (1978). Apart from providing a realistic baseline for the subsequent interpretation of geographic and taxonomic trends and the assessment of relative contributions of population factors, variance partitioning is also useful in determining the relative taxonomic value of characters (Straney 1978; Leamy 1983). If the aim of the study is to compare individuals across populations (as is usually the case) and eliminating or adjusting for extraneous sources of variation due to factors such as age or sex, then characters showing the smallest variances for these factors, but with large error variances, are the most appropriate. Characters utilized in this study were selected on the basis of the morphological integration concept (Olson & Miller 1958; Moss & Young 1960; Moore 1981; Cheverud 1982; Taylor 1990; Taylor & Meester 1993). In the *% SSQ* analyses, their generally large error components place confidence in the systematic usefulness of the selected characters.

Based on the 'four tooth-wear class' analyses, overall *% SSQ* values due to sex and age in the current study are generally lower than those reported both by Leamy (1983), who used a similar approach, and Straney (1978), who used the variance components approach. Leamy (1983) suggested that such differences may be a function of the type of characters used. Unlike this study, these two studies included appendicular characters. It has been demonstrated that appendicular characters exhibit higher growth rates than axial characters (Leamy & Bradley 1982). Although his conclusion was restricted to the age component, Leamy (1983) suggested the existence of a direct proportionality between characters with higher growth rates and larger variance components. The *% SSQ* contributions in this study are comparable to those found in *Cynictis penicillata* (Taylor & Meester 1993), a study restricted to axial characters.

In spite of relatively small sample sizes in the present study, a useful picture emerges from parallel univariate and multivariate analyses. The approach adopted here is useful as a preliminary step to any morphometric study, and the differentiation of some tooth-wear classes cautions against either arbitrary decisions or superficial evaluations of non-geographic variation.

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Appendix 1 *Aethomys* specimens examined (all in Transvaal Museum, Pretoria)

Aethomys chrysophilus: Farm Al-te-ver, 1 km SSE Maasstroom, Transvaal, South Africa (22°46'S, 28°28'E): 9 males (TM 26474, 26486, 26541, 26557, 26559, 26562, 26612, 26667, 26684); 13 females (TM 26492, 26510, 26514, 26540, 26561, 26565, 26574–75, 26583, 26585, 26611, 26668–69). Olifantspoort Farm 328, 19,2 km S Rustenburg, Transvaal, South Africa (25°46'S, 27°16'E): 13 males (TM 19614–16, 19618, 19632, 19648–49, 19651, 19656, 19672–75); 8 females (TM 19633–34, 19640–42, 19650, 19670–71).

Aethomys namaquensis: Boekenhoutkloof, Transvaal, South Africa (25°31'S, 28°30'E): 25 males (TM 30430, 30432–34, 30439–42, 30959–60, 30967, 30969, 30971–73, 30975–77, 30979, 30984, 31259, 31262–64, 31267); 23 females (TM 30428, 30431, 30435–38, 30458, 30961–64, 30966, 30968, 30970, 30974, 30980–83, 31258, 31261, 31265–66). Farm Narap, 28 km SSE Springbok, Cape Province, South Africa (29°53'S, 17°45'E): 15 males (TM 27795, 27801, 27811–13, 27836–38, 27841, 27843, 27878, 27906, 27945, 27948, 28006); 17 females (TM 27794, 27798–27800, 27808–09, 27831–34, 27842, 27877, 27907–08, 27946–47, 28007).